AGE-SPECIFIC DIFFERENCES IN THE BREEDING BEHAVIOR AND ECOLOGY OF THE AMERICAN REDSTART

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MATURATION rates in birds are controlled by natural selection (Lack, 1954; Orians, 1961; Amadon, 1964; Selander, 1965). Slow maturation rates evolved in species where there is strong intraspecific competition for food (Amadon, 1964), species with high population densities (Orians, 1961; Wynne-Edwards, 1962) and in some icterid species as an outcome of a polygamous mating system (Selander, 1965). The American Redstart (*Setophaga ruticilla*) has a slower maturation rate than other parulids, many males not breeding until their second spring. The purposes of this paper are (1) to investigate the relationship between age of males (first-year vs. older) and type of habitat utilized, and (2) to suggest the proximate and ultimate factors responsible for the complex relationships of plumage, behavior, and ecology in this species and some other passerines.

The American Redstart has an extensive breeding range and in many areas is one of the most abundant breeding birds. It is found in a variety of habitats including willow and alder thickets, deciduous, mixed deciduous and coniferous, and even primarily coniferous forests (Bent, 1953). The biology of the redstart is of special interest in relation to the evolution of adaptations leading to success as measured by broad geographic range, utilization of a variety of habitats and high population density.

METHODS

This study was conducted in two different areas. Reproductive behavior was studied from the arrival of males until the fledging of young in a deciduous swamp forest in Ithaca, New York. This stand was dominated by a nearly closed canopy of mature deciduous trees and an understory of saplings which reached 20 feet in height. Dense stands of saplings occurred in areas where the canopy was interrupted. Redstarts occurred in both types of habitats. Information was obtained on the relative number of first-year males, their behavior, and mating success.

Censuses of redstarts in a variety of habitats in Maine were conducted between 10 June and 19 June 1965, near Damariscotta (Lincoln Co.) and in the primarily coniferous forests on Mt. Desert Island (Hancock Co.). Since first-year males arrived later than older males, we selected the initial date of the census late enough to insure that all breeding males had arrived. All of the males censused behaved like territorial birds, singing loudly in a restricted area. Although we saw the mates of some birds, both first-year and older, it was not possible to determine the proportion of mated birds.

After hearing a male sing, its immediate habitat was described; then the bird was approached and its age determined on the basis of plumage.

Habitats in Maine were classified in the following manner: (1) deciduous forests—some trees taller than 30 feet, an understory of saplings to 20 feet and sometimes up to 10 per cent conifers (white pine, spruce); (2) immature deciduous forests—tallest trees smaller than above, understory not as well developed and often more open; (3) alder thickets—dense shrub growth usually to 15 feet in height, often with some willow and other deciduous growth; (4) mixed forest—more than 10 to 60 per cent conifers (white pine, and/or spruce), with rest deciduous; (5) coniferous forest—more than 60 per cent coniferous, including some virtually pure spruce forest.

All the New York birds occurred in habitat categories 1 and 2; no effort was made to distinguish between them.

OBSERVATIONS

Molt and plumage.—A hand-raised male and female were observed from eight days of age until 10 months. The male obtained a few black spots on the face and breast during the first pre-alternate molt in early spring but otherwise retained a female-like plumage. This observation supports the assertion in the literature that first-year males retain a female-like plumage but generally with additional black feathers on the breast and chin, lores, cheeks, or crown (Chapman, 1907). Unfortunately we were unable to follow this male through the pre-basic molt in the fall, but according to Chapman (1907) the adult male plumage is attained at this time. The possibility remains that some first-year males molt into adult plumage at their first pre-basic molt or that some males are delayed beyond the end of their first breeding season in attaining adult male plumage. Ossification of the skull progresses more slowly in the redstart than in most other parulids (S. Eaton, pers. com.). David Bridge (pers. com.) reports that there are rare cases of males in immature plumage during the fall migration which had completely ossified skulls, indicating that at least some males do not attain adult male plumage until their third pre-basic molt. However, for the purpose of this study, we term males with a female-like plumage "first-year." They are easily distinguished from females in the field by the presence of a few black spots.

First-year females in the spring often show less yellow in the wing than older females (Chapman, 1907) and our captive bird also had less yellow on the sides of the breast. Birds with these characters which were observed in the field were considered to be first-year females. However, it is not known if all first-year females have this plumage or if older females also sometimes do.

Time of arrival on territory.—The usual order of arrival, although there was some overlap, was older males, older females and first-year males. The arrival time of first-year females was less certain but some arrived after the first-year males. The delay between the mean arrival date of the older males and first-year males was about two weeks in both New York and Maine.

Territorial behavior.—Redstarts are very aggressive and maintain rather rigid territories, tolerating no intrusion by conspecific males (Ficken, 1962a). Displays and fighting are common. The redstart is more aggressive than several other parulids which we studied (*Dendroica petechia, D. pensylvanica, D. virens, Vermivora pinus*, and *V. chrysoptera*) (Ficken and Ficken, 1965). In New York, older males first settled on territories in tracts of mature forest. Later, when first year males arrived, only peripheral areas, usually where the forest was open and low in stature, were available. The young males were usually restricted to these peripheral habitats by the aggressiveness of the older males. Older males appeared to be more aggressive than the young; they always won encounters with younger males.

Territory size.—Little is known about the territory size of first-year males as compared to older males. However, in the New York study area we found that the territory size of the two age classes was not markedly different, except that the smallest territory observed belonged to a first-year male. Hickey (1940) also noted that the territory size of the two age classes was similar.

Redstart territories are quite small when compared to those of other warblers (Mayfield, 1960) even those coniferous forest species during spruce budworm outbreaks (Kendeigh, 1947). In our New York study area they averaged about 0.75 acres, and Hickey (1940) reports territories were one acre or less on a "heavily wooded slope" in Westchester County, New York. Sturm (1945) found very small territories; one group in a second growth deciduous forest averaged 0.24 acre and another 0.16 acre. Thus deciduous woodlands with much second growth appear to be optimal for the species as such habitats support the maximum population densities. However, most territories in mixed and coniferous forests in Maine were over an acre in size and even in the deciduous habitats many males were isolated or had only one neighboring male in an area of several acres.

Mating success.—All older males (52) in our New York study area obtained mates while only three out of 7 (43 per cent) first-year males did so (Ficken, 1962a). Similarly, Sturm (1945) noted that only three out of 5 (60 per cent) first-year males were mated in an Ohio woodland. However, the four first-year males studied by Hickey (1940) obtained mates. In our New York study area, first-year males that did not obtain mates remained only about two weeks on territory, then left.

Floaters.—In other species of warblers it has been shown that there is a

population of non-breeding males which will occupy territories when space is available (Stewart and Aldrich, 1951; Hensley and Cope, 1951). First-year male redstarts are sometimes "floaters," at least in deciduous woodlands. We have on several occasions seen unmated males in sub-optimal habitats in June. Each was there for a few days and usually silent or singing only muted song fragments. Hickey (1940) reports a first-year male that was singing softly and was "furiously driven off by males and females whenever it passed through their territories." Some of these floaters may not have found suitable areas for the establishment of territories because of the aggressiveness of older males. Others may have abandoned territories when they did not obtain mates. There is also the possibility that some first-year males do not even attempt to set up territories but are floaters from the start.

Nesting success.—We did not obtain quantitative data on nesting success in the two age classes but have a few observations which show that pairs of first-year birds are less successful. One such pair constructed and subsequently abandoned seven nests, at least twice after the female had begun incubation. Finally, this pair left the area in late July and presumably made no further breeding attempts that year. The cause for the nest abandonments was not known, but this behavior was not noted in older pairs. The nest of another first-year female was blown away by winds that destroyed no other nests in that area. This was probably due to its insecure anchorage, since the female had selected a two-pronged rather than a typical three-pronged crotch (Ficken, 1964).

Foraging behavior.—It is generally agreed that redstarts prefer deciduous woodland with a good undergrowth of bushes and young trees (Chapman, 1907; Bent, 1953; Griscom and Sprunt, 1957). Redstarts forage at medium elevations, usually between 10 and 30 feet, but occasionally near the ground or on low herbaceous plants (Ficken, 1962b). Insects are obtained by gleaning, hovering, and flycatching. Flycatching makes up over 80 per cent of the foraging patterns before the leaves are out in May, but the other patterns are more prevalent as the season progresses.

Relation of age and habitat.—The relative number of first-year territorial males in deciduous woodlands in New York and Ohio is surprisingly small, averaging 12 per cent in the three studies with large samples of birds (Table 1). Table 2 shows the incidence of first year males in a variety of Maine habitats. Deciduous forests in Maine contain a higher percentage of first-year males than do deciduous forests in New York and Ohio but are comparable to the findings for Michigan. There are differences in the frequency of first-year males in different habitats in Maine. First-year males are least common in alder thickets and relatively mature deciduous forests and more common than older males in immature deciduous, mixed, and coniferous

forests. The difference between the number of first-year males in deciduous and mixed forests is statistically significant ($P < 0.05$) while that between alder and deciduous is not ($P > 0.05$). Numbers were insufficient for a statistical analysis of mixed vs. coniferous and deciduous vs. immature deciduous forests.

The distribution of the two age classes of redstarts in Maine habitats appears to be related to the amount of deciduous foliage. Habitats which have a high deciduous foliage density in the vertical foraging range of the redstart are alder and mature deciduous. Immature deciduous (often more open) and mixed woodlands are intermediate. Of course, forests consisting of more than 60 per cent conifers have the lowest deciduous foliage density. The frequency of first-year males parallels this foliage density, being higher where the deciduous foliage density is lower. MacArthur et al. (1962) suggested that species abundance in birds is related to the foliage density of vegetation in deciduous forests and this example shows that age classes within a species may also be so related.

DISCUSSION

Our hypothesis is that originally, before the evolution of a special plumage, first-year males had lower reproductive success than older males. Such a situation exists in many birds and is probably widespread (e.g., Nice, 1937; Snow, 1958; Coulson and White, 1958; Wynne-Edwards, 1962). For example, in Song Sparrows (*Melospiza melodia*) first-year males often arrive later than older males, are less aggressive, and in many cases their females lay fewer eggs than older ones (Nice, 1937).

With intense intraspecific competition, those individuals which were the least efficient would produce too few young to balance the "expense" of breeding. Selection would favor a system for lowered reproduction in young birds if this led to enhanced reproductive success in subsequent years. The first evolutionary step is probably the establishment of a hormonal mechanism. Some support for this is found in studies of Red-winged Blackbirds (*Agelaius phoeniceus*). Testes of first-year males, which usually do not breed, attain their maximum development three weeks after older males. Also their maximum size is only two-thirds that of older males, although they do undergo spermatogenesis (Wright, 1944). A lowered hormone level and a delay in testes development might have many effects in first-year birds including lowered aggressiveness, later arrival on the breeding grounds and retention of a female-like plumage.

In many species molt into breeding plumage is at least partly controlled by androgens (Witschi, 1961). Miller (1933) suggested that the great variability in melanin deposition in first-year male Phainopeplas (*Phainopepla*

TABLE 1

PERCENTAGE OF TERRITORIAL FIRST-YEAR MALES IN DECIDUOUS HABITATS

Per cent territorial first-year males	Total number of males	Habitat	Reference
12	59	deciduous—N. Y.	Ficken, 1962a
0	10	mixed—N. Y.	Kendeigh, 1945
8	48	deciduous—N. Y.	Hickey, 1940
29	7	deciduous—Mich.	Baker, 1944
15	34	deciduous—Ohio	Sturm, 1945

nitens) was due to a variable amount of testicular hormone at the time of the molt. The possession of a female-like plumage in first-year males which do not breed probably has not been selected for directly but is the outcome of selection for slower maturation (Orians, 1961). The plumage of the first-year male redstart seems to confer no direct advantage in the competitive situation with older males since first-year males are reacted to just as aggressively as older males. Male redstarts also react very aggressively toward females initially (Ficken, 1963) and this again illustrates that a female-like plumage is reacted to aggressively. Since first-year males sing, this probably enhances their aggressive releasers as compared to females. In Orchard Orioles (*Icterus spurius*) which also have a female-like plumage their first year (but it is not known what proportion of first-year males breed) fights between first-year and older males are intense, although the species is in general non-territorial (Dennis, 1948). Thus, first-year male plumage in this species as well apparently does not reduce aggression by other males. It might be expected that it would be advantageous for floaters not to be reacted to aggresively by other males, but as Hickey (1940) observed, redstart floaters are attacked despite their plumage. However, a female-like plumage is much more cryptic than the red and black of the adult male, at least to the human observer, and this crypticity might be of value in reducing predation on first-year males.

Later arrival may lead either to failure to procure a mate or to mating with first-year females. Since first-year males arrive later than most females, mating may be partly a matter of availability of females at the time of arrival of males. However, other factors are probably involved. Females may not be as sexually responsive to males in a female-like plumage. Also the lowered aggressiveness of first-year males may reduce chances of pairing since an initial strong aggressive response of the male toward the female may be necessary for pair formation to occur in this species (Ficken, 1963).

Late arrival may contribute to the inability of first-year males to compete successfully with older males in several ways. One is that often all suitable

TABLE 2

FREQUENCY OF TERRITORIAL FIRST-YEAR MALE REDSTARTS IN A VARIETY
OF HABITATS IN MAINE

Habitat	Total no. of males	No. of first-year males	Percentage of first-year males
Alder	14	1	7
Deciduous	14	3	21
Immature deciduous	7	5	71
Mixed coniferous-deciduous	15	9	60
Coniferous	11	9	82

territories are occupied. Another is that all older males are recently mated and territorial aggressiveness seems to reach its peak at just that time (Ficken, 1962a) so they are likely to be more aggressive to first-year males than they were to each other initially.

The reduced aggressiveness of the first-year males probably also affects their ability to obtain suitable territories. Experience plays a part in success in aggressive encounters of many animals (Scott, 1958), and lack of experience probably reduces success in encounters between first-year and older male redstarts. The inability to compete successfully with older males probably leads to some wandering and males either become floaters or sub-optimal habitats are found and territories are established there where competition with other males is reduced or absent. First-year male redstarts are more often found in late spring outside their normal breeding range in California than are older males (Root, 1962), indicating that the young males are probably the pioneers in range and habitat extensions. The utilization of sub-optimal habitats probably reduces breeding success further. One way may be through reduction of the amount of food available since the deciduous foliage density is lower. In some species choice of a mate by the female is at least partially determined by the quality of the habitat of potential mates (Verner, 1963; Tompa, 1962). If this is true in the redstart, mating success will be further reduced by the possession of territories in sub-optimal habitats.

Thus the ultimate cause of the interrelated effects of female-like plumage, low reproductive success, less aggressive behavior and utilization of sub-optimal habitats is selection against breeding of what were originally slightly less successful birds. The question naturally arises as to why first-year males attempt to breed at all. However, if they breed where they are not competing with older males, and even some small fraction is successful, this would be advantageous. Also, there may be much learning necessary for reproductive success. By attempting to breed or just getting through some of the stages

of breeding, first-year males may have a better chance for breeding in sub-sequent years as a result of this experience (Selander, 1965).

Many aspects of the redstart system are not unique. Wynne-Edwards (1962) has pointed out that slow maturation rates are often found in species with high population densities. However, he postulates a system based on group selection while it probably can best be explained by natural selection at the individual level (Amadon, 1964; Selander, 1965), as a result of the system older and more experienced breeders having reduced competition for territories. Orians (1961) studied the population structure of blackbirds (*Agelaius phoeniceus* and *A. tricolor*) and extended his conclusions to other species as well. He suggested that slow maturation of first-year males is "characteristic of species in which breeding sites are limited. Probably these are all species which are ineffectively controlled between breeding seasons so that surpluses of breeding birds are regularly present." Selander (1965), from his studies of polygamous *Cassidix* species suggests that "because the probability of a young male obtaining mates in competition with older experienced males is very low, males which postpone breeding may ultimately have greater reproduction; and through selection first-year males have become adaptively 'handicapped' physiologically and morphologically in competition with adult males for mates."

Delayed maturation occurs in some icterids (Orians, 1961; Selander, 1965) and although in some cases it seems to be associated with a high population density the situation is further complicated by the type of mating system, delayed maturation being more common in non-monogamous species, although this is probably a consequence rather than a cause of delayed maturation (Selander, 1965). For example, delayed maturation occurs in the grackles *Cassidix major* and *C. mexicanus* which have a plumage intermediate between the juvenile-female and the adult male, and the males do not breed until their second year (Selander, 1965). The Red-winged Blackbird (*Agelaius phoeniceus*), the Tricolored Blackbird (*A. tricolor*), and the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) have delayed maturation, are colonial with high breeding densities and breeding sites are at a premium in some localities. Male Red-winged Blackbirds do not normally breed until two years of age, although first-year males may occur at the periphery of the colony. Some obtain territories and a few breed. In the Tricolored Blackbird yearling males regularly establish territories, but as in the redstart they are crowded into the less desirable sites and are less successful in obtaining mates (Orians, 1961).

Orians' hypothesis of a relationship between high breeding population densities and delayed maturation seems to be applicable to cases where there is little information available on breeding behavior. For example, a delay

in attaining adult male plumage occurs in the Orchard Oriole (*Icterus spurius*) but not in the Baltimore Oriole (*I. galbula*), and the Orchard Oriole seems to have intense intraspecific competition in some areas. For example, Dennis (1948) reports that males of this species are not territorial and one population which he studied attained a density of 114 males in 7 acres, with as many as 20 nests in one tree. The female-like plumage of first-year male crossbills *Loxia curvirostra* and *L. leucoptera* may also be related to locally high population densities in these semicolonial breeders. First-year male Purple Martins (*Progne subis*) differ in plumage from older males. This species nests in colonies, and there is probably also a shortage of nest sites.

The species with delayed maturation which we have discussed are those in which there is a color difference between the age classes and non-breeding first-year males are more noticeable. However, there are cases such as that noted by Selander (1964) where some species of the wren genus *Campylorhynchus* breed the first year while others do not. Whether this is related to breeding population densities and intraspecific competition is not known.

The evolution of delayed maturation rates in birds might be expected more commonly in species with a long life span as is the case with certain sea birds, many of which do not breed until they are several years old (e.g., Wynne-Edwards, 1962). These species also often have high population densities. In such species the enhancement of breeding success in older birds by reduced competition with younger ones would occur over several breeding seasons, although there are undoubtedly many other variables influencing their reproductive success. However, it is probably not surprising that relatively few of the small passerines, with their relatively short life span, have evolved such a system.

Our findings also have implications for studies of habitat "preference." The habitat difference between first-year and older males is obviously not innate. However, in the species as a whole there is probably an innate basis, although with learning also involved, for responding only to certain types of habitats. Even first-year males are selective, and are not found breeding in just any habitat. It is misleading to refer to a "preference" or "selection" in the case of first-year redstarts. They often seem to initially occupy habitats where older males are also breeding but through competition must go elsewhere. It would seem advantageous for a species to be somewhat flexible and to be able to respond to a variety of habitats (Svärdson, 1949).

Thus the redstart has evolved a system of interrelated physiological, behavioral, and ecological adaptations which are related to intraspecific competition and to its extensive and diverse geographic range and which contribute to making it one of the most successful North American passerines.

Other species with intense intraspecific competition may have similar systems, although differing in some respects from that proposed for the redstart.

SUMMARY

First-year male American Redstarts are relatively uncommon as compared to older males as breeders in deciduous forests in the eastern and central United States. However in Maine they occur more frequently than older males in sub-optimal habitats. In New York first-year males arrive later than older males, are less aggressive and consequently at a disadvantage in competing with older males for territories in optimal habitats. They are also less successful in obtaining mates, at least partly due to their later arrival. A system is proposed to explain the interrelated effects of a female-like plumage, late arrival, lowered aggression, and use of sub-optimal habitats. It is suggested that delayed maturation, probably involving a lowered androgen level, evolved as a result of intense intraspecific competition in this species, and that selection acts against first-year males breeding in optimal habitats. Other passerines in which first-year males differ in plumage from older males also have high population densities and were probably subjected to similar selective pressures.

ACKNOWLEDGMENTS

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